AN ANOMALOUS POPULATION OF *ASTER* (ASTERACEAE: ASTEREAE) SENSU LATO IN MICHIGAN

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ABSTRACT

Plants from a single population on the Keweenaw Peninsula in Houghton County, Michigan, have been reported as hybrids between *Doellingeria* (*Aster*) *umbellata* and *Oclemena* (*Aster*) *nemoralis*, but the few features of putative intermediacy between these two species are equivocal. In contrast, morphological features of their roots, leaves, capitulescence, florets, and cypselae are consistent with those of *Oclemena*—in the interpretation here, morphological evidence for the genomic contribution of *Doellingeria* is very limited, and the Keweenaw plants more likely arose from within *Oclemena*. They are suggested to represent either an atypical form of *O.* ×*blakei* (a recurring and persistent hybrid between *O. nemoralis* and *O.* (*Aster*) *acuminata*) or a relict population differentiated earlier in the evolutionary history of the genus and appropriately recognized as a separate species. Current evidence is insufficient to convincingly support a single hypothesis of origin.

RESUMEN

Plantas de una sola población en la Península de Keweenaw en el Condado de Houghton, Michigan, se han citado co híbridos entre *Doellingeria* (*Aster*) *umbellata* y *Oclemena* (*Aster*) *nemoralis*, pero las pocas características presumiblemente intermedias entre estas dos especies son equívocas. En contraste, las características morfológicas de sus raíces, hojas, capitulescencia, flósculos y cipselas coinciden con los de *Oclemena*—en la interpretación que hacemos aquí, las evidencias morfológicas de una contribución de *Doellingeria* es muy limitada, y las plantas de Keweenaw probablemente surgieron de *Oclemena*. Se sugiere que representan ya sea una forma atípica de *O.* ×*blakei* (un híbrido recurrente y persistente entre *O. nemoralis* y *O.* (*Aster*) *acuminata*) o una población relicta diferenciada tempranamente en la historia evolutiva del género y reconocida apropiadamente como una especie independiente. Las evidencias actuales son insuficientes para apoyar una hipótesis única de su origen.

The recent report (Gerdes 1998) of a population of hybrids between *Doellingeria* (*Aster*) *umbellata* (P. Mill.) Nees and *Oclemena* (*Aster*) *nemoralis* (Ait.) Greene from the Keweenaw Peninsula of Lake Superior in northwestern Michigan is remarkable. Such an intergeneric hybrid would provide corroborative evidence that these two genera (*Doellingeria* Nees and *Oclemena* Greene) segregated from *Aster* are closely related. Naturally occurring intergeneric hybrids in the Astereae have previously been reported only between closely related genera—in some cases these hybrids may be better interpreted as between congeneric species (Nesom 1994b).

A hypothesis of close relationship between *Doellingeria* and *Oclemena* (Nesom 1994a) is based on morphological similarities. In contrast, molecular evidence (Semple et al. 1996; Xiang & Semple 1996) suggests that *Oclemena* may

SIDA 19(3): 625 – 632. 2001

be closely related to *Ionactis* Greene. A hypothesis of close relationship between *Doellingeria* and *Oclemena* also is suggested in the disparity of interpretation regarding the position of *Aster reticulatus* Ell., a southeastern USA endemic placed by Semple et al. (1991, 1996) in *Doellingeria* but by Nesom (1993, 1994a, 2000) in *Oclemena*. Hybridization between species of *Doellingeria* and *Oclemena* has not been previously reported, although *D. umbellata* and *O. nemoralis* are sympatric over most of the range of the latter and both species occur in wetland habitats.

Gerdes noted that the putatively hybrid population was distinctive in the field and appeared to be intermediate between nearby populations of *Doellingeria umbellata* and *Oclemena nemoralis*. While the putative hybrids clearly do not fit the typical morphology of either species, the only indication of intermediacy in the published observations is in the statement (p. 18) that the "overall height and leaf size and shape are intermediate between the assumed parents." In the illustration and description, and in the voucher specimens, other possible indications of intermediacy between *D. umbellata* and *O. nemoralis* are equivocal.

Plants studied

The population described by Gerdes (*Gerdes 2210*) includes about 20 plants in a tamarack swamp situated between populations of *Doellingeria umbellata* ("common 60 m north of the hybrid site in a mixed wetland complex"—*Gerdes 2211*) and *Oclemena nemoralis* (ca. "60 m southeast of the hybrid site in a swale"—*Gerdes 2209*). Two plants of the putative hybrids and one plant each of *D. umbellata* and *O. nemoralis* from the Houghton County site were available for study (MICH), as well as many other specimens from taxa of *Oclemena* and *Doellingeria* (BRIT, GH, NCU). The two plants of *2210* are virtually identical in micromorphological detail, perhaps representing a single clone, and Gerdes did not note the occurrence of significant variation among the putative hybrids. The plant of *O. nemoralis* is morphologically typical of the species—this collection represents the westernmost known population of the species (see Voss 1996; Gerdes 1998). The collection of *D. umbellata* may be arbitrarily identified as var. *umbellata*; hairier plants of the species (*D. umbellata* var. *pubens* (A. Gray) Britt.) also occur on the Keweenaw Peninsula (as mapped by Semple et al. 1991).

Houghton County specimens examined:

1) Doellingeria umbellata (P. Mill.) Nees—MICHIGAN. Houghton Co.: Grand Traverse Bay ridge and swale complex, ca. 7 mi ESE of Lake Linden, travel E of Rice Lake ca. 0.6 mi and walk N of gravel road into swale, edge of sandy road and *Sphagnum*/ericaceous swale; *Aster nemoralis* also in swale; rays creamy white; 18 Sep 1997, *L.B. Gerdes 2211* (MICH).

2) *Oclemena nemoralis* (Ait.) Greene—MICHIGAN. Houghton Co.: Grand Traverse Bay ridge and swale complex, ca. 7 mi ESE of Lake Linden, and E of Rice Lake. Swale, primarily a *Sphagnum*/ericaceous bog (poor fen); plants scattered and numerous with *Carex michauxiana*, *Carex oligosperma*, *Andromeda glaucophylla*, etc.; rays dark pink; 18 Sep 1997, *L.B. Gerdes 2209* (MICH).

3) The putative hybrid—MICHIGAN. Houghton Co.: Grand Traverse Bay ridge and swale complex, ca. 7 mi ESE of Lake Linden and E of Rice Lake. Tamarack swamp adjacent to a *Sphagnum*/ericaceous swale; ca. 20 plants with *Aronia prunifolia*, *Chamaedaphne calyculata*, *Alnus rugosa*, *Calamagrostis canadensis*, and *Carex oligosperma*, *Aster nemoralis* and *Aster umbellatus* nearby; rays light pink; 18 Sep 1997, *L.B. Gerdes 2210* (MICH—2 sheets).

Evidence for the *Doellingeria* genome

Consideration of the illustration and published description of *Gerdes 2210* and examination of the voucher specimens indicate that features of putative intermediacy between *Oclemena nemoralis* and *Doellingeria umbellata* are relatively few.

Height.—Plants of *2210* are 6–7 dm tall, generally between the range of height for *O. nemoralis* (2–7 dm) and *D. umbellata* (3–20 dm) but also at the top of the range for *O. nemoralis* as well as *O. acuminata*.

Leaves.—Leaves of *2210* are narrowly elliptic, 4.5–5.5 cm long and 7–10 mm wide, with entire, barely revolute margins. Leaves of *D. umbellata* are elliptic to narrowly elliptic, mostly 6–12 cm long, 10–25 mm wide, and flat-margined; those of *O. nemoralis* are very narrowly oblong to linear-lanceolate, mostly 2–5 cm long, 2–12 mm wide, with entire, strongly revolute margins. Leaves of *2210* are intermediate in size between *D. umbellata* and *O. nemoralis* but they are more similar in shape to those of *D. umbellata*. The abaxial surfaces of *2210* are minutely sessile-glandular and could be regarded as intermediate between the glandular (larger glands) surfaces of *O. nemoralis* and eglandular surfaces of *D. umbellata*; the glandularity of *2210*, however, also appears to be indistinguishable from that of plants hybrid between *O. nemoralis* and *O. acuminata* (see below).

Ray florets.—Rays of *2210* are pink, intermediate between the purple of *O. nemoralis* and white of *D. umbellata*; pink rays also are characteristic of hybrids between *O. nemoralis* (purple-rayed) and *O. acuminata* (white-rayed). The length of the rays intermediate between *O. nemoralis* and *D. umbellata* but within the range of variation for *O. nemoralis*.

Cypselar vestiture.—Cypselae of *2210* are densely strigose-hispid, more similar to the sparsely to densely strigose cypselae of *D. umbellata* than the typically glabrous ones of *O. nemoralis* (thus this aspect of vestiture is technically not intermediate). Otherwise, the densely sessile-glandular cypselar surfaces

of *2210* are similar to those of *O. nemoralis* but not to the eglandular surfaces of *D. umbellata*.

Morphological evidence that *Doellingeria umbellata* is represented in the genome of the plants of *Gerdes 2210* is limited, represented by the features of equivocal interpretation noted above. In contrast, various features of the roots, leaves, capitulescence, florets, and fruits refer *Gerdes 2210* to *Oclemena*. The comparisons in Table 1 summarize morphological distinctions between *Oclemena nemoralis* and *Doellingeria umbellata*—these also are essentially the contrasts that distinguish the two genera (see Nesom 1994a). In each contrast, the morphology of *2210* is similar to that of *Oclemena*.

If the assessment here of *Gerdes 2210* is correct in excluding *Doellingeria* from its close ancestry, two alternative hypotheses would place the evolutionary origin of this anomalous population from within *Oclemena*. First, it may represent a hybrid between *O. nemoralis* and *O. acuminata* (Ait.) Greene, or second, it may represent a lineage of *Oclemena* differentiated early in the evolutionary history of the genus and now persisting only as a relict at the Houghton County site.

Identification as *Oclemena* ×*blakei*

The plants of *Gerdes 2210* are nearly identical in overall aspect to some individuals of *Oclemena* ×*blakei* (Porter) Nesom, a fertile, recurrent, and persistent hybrid between *O. nemoralis* and *O. acuminata*—compare Fig. 1 of Gerdes (1998) to Figs. 3 and 11 of Pike (1970). Populations of *O.* ×*blakei* are scattered through the area of sympatry of the parents where ecological conditions allow their close contact (Brouillet & Simon 1981). "Extensive colonies of [*O.*] ×*blakei* are often found at the edges of bogs, the shores of ponds, and swampy borders of woods, etc., the kinds of areas that are intermediate in wetness between the boreal forest habitat of [*O.*] *acuminata* and the open bogs of [*O.*] *nemoralis*" (Pike 1970, p. 401).

If the plants of *Gerdes 2210* are scored on the morphological hybrid index developed by Pike (1970; also see Hill & Rogers 1973; Brouillet & Simon 1981), the value is 9 (Table 2), which is within the range characteristic of *O.* ×*blakei*, intermediate between *O. nemoralis* and *O. acuminata*. *Oclemena* ×*blakei* is known to produce fertile seeds (Hill & Rogers 1973), but it was not possible to make unequivocal observations of fertility for *Gerdes 2210*. Pollen grains on the stigmatic surfaces were regular in size, but the anthers had opened before the collection and an estimate of pollen fertility could not certainly exclude pollen from other species. None of the cypselae of *Gerdes 2210* were completely mature when collected; dissected cypselae examined from each plant had produced an elongated but otherwise undeveloped embryo. *Oclemena* ×*blakei* and its parental species are known to have a chromosome number of $2n = 18$ (Hill & Rogers 1970). Scoring of *2210* on this hybrid index does not indicate that it

TABLE 1. Morphological contrasts between *Oclemena nemoralis* and *Doellingeria umbellata* and the plants of *Gerdes 2210*.

	Oclemena nemoralis	**Gerdes 2210**	**Doellingeria umbellate**
Root System	slender, elongate rhizomes, without a cluster of thick, fibrous roots	slender, elongate rhizomes, without a cluster of thick, fibrous roots	dense cluster of thick fibrous roots at the sub-caudex or crown, also with eleongate-rhizomes
Leaves	glandular abaxially	glandular abaxially	eglandular
Peduncles	long, flexuous	long, flexuous	short, stiff
Ray Corollas	pink to purple, 11–18 mm long, strongly coiling	pink to purple, 10–12 mm long, strongly coiling	white, 5–9 mm long, not coiling
Disc Corollas	narrowly tubular-funnelform, slightly widened above the tube; lobes cut ca. 1/3 of limb, erect to spreading	narrowly tubular-funnelform, slightly widened above the tube; lobes cut ca. 1/3 of limb, erect to spreading	broadly funnelform, abruptly widening above the tube; lobes cut nearly to base of limb, reflexing-coiling
Cypselae	sessile-glandular, otherwise glabrous, fusiform to narrowly columnar, ca. 1/2–2/3 the phyllary length at maturity	sessile-glandular, strigose-hispid, fusiform to narrowly columnar, ca. 1/2–2/3 the phyllary length at maturity	eglandular, strigose, obovoid, nearly equal the phyllary length at maturity
Pappus	inner and outer series of +- even length	inner and outer series of +- even length	outer series of short (<1 mm) setae

TABLE 2. Morphological hybrid index for *Gerdes 2210*.

Character	**State**	**Value**
No. of leaves	35–100	0
Internode length (mm)	9–11	1
Ratio leaf length/width	5–4	2
Leaf margin—revoluteness	+-flat	2
Leaf margin—scabrosity	intermdt	1
Leaf margin—toothing	entire	0
No. of bracts per peduncle	2–4	1
No. of heads per capitulescence	2+	1
Ray color	pink	0
Zebra hairs on stem	occur	1
	Hybrid index value = 9	

actually is a hybrid between *O. nemoralis* and *O. acuminata* but does show that its features can be interpreted as intermediate in the same way as those of known hybrids can be.

Two conditions complicate the identification of *Gerdes 2210* as *Oclemena ×blakei*: **(1)** *O. ×blakei* previously has been found only within the area of sympatry of the parents, and one of the parental species, *O. acuminata*, does not occur in the Keweenaw region; and **(2)** plants of *Gerdes 2210* have entire leaves and hispid cypselae, features not generally characteristic of *O. ×blakei*.

(1) *Oclemena ×blakei* has been known to occur only much further east—the closest known locality to the Keweenaw site is in southeastern Ontario, about 850 kilometers eastward (maps in Brouillet & Simon 1981, Semple et al. 1966). The closest known locality for *O. acuminata* is the same region of Ontario. *Oclemena nemoralis* grows immediately adjacent to the *2210* population, but it is unlikely that *O. acuminata* has occurred naturally in Michigan since postglaciation revegetation (Brouillet & Simon 1981). Long-distance dispersal would the most likely explanation for the far-disjunct occurrence of *O. ×blakei* on the Keweenaw Peninsula—at least it is a simpler hypothesis than a postulate of the former occurrence and extirpation of *O. acuminata* far west of its present geographic range. "Long-distance dispersal and chance establishment in suitable bogs ... are probably responsible for [the] establishment [of *O. nemoralis*] in the eastern Lake Superior area ... and the species could still be expanding its range westward ..." (Brouillet & Simon 1981, pp. 539–540). The discovery of *O. ×blakei* at the westernmost locality of *O. nemoralis* might also suggest that the former is similarly expanding its range.

In the region of parental sympatry, *O. ×blakei* often occurs with only one of the parents or even with neither of the parents in close proximity (Pike 1970), apparently persisting through its rhizomatous habit and ranging more widely through fertile cypselae. When found with only one of its putative parents, *O. ×blakei* is more often associated with *O. nemoralis* (Pike 1970; Brouillet & Simon 1981), perhaps because of their greater similarity in habitat.

(2) The parentage of *O. acuminata* in the hybrid *O. ×blakei* is usually reflected by at least some degree of foliar toothing. Entire leaves occur rarely in *O. ×blakei*, but F1 individuals may sometimes be closer in morphology to the entire-leaved *O. nemoralis* than to the toothed-leaved *O. acuminata* (Pike 1970; Hill & Rogers 1973). Evidence for introgression between *O. ×blakei* and its parents was observed in nature by Pike (1970) and experimentally duplicated by Hill and Rogers (1973), but the overall morphology of *Gerdes 2210* is more similar to an F1, except for the entire leaves. Leaves of *2210* are elliptic—those of *O. ×blakei* vary in shape from oblanceolate (broadest above the middle) to elliptic.

The cypselae of *Gerdes 2210* bear a mixture of sessile glands and numerous, slender, spreading-ascending, sharp-pointed hairs and are closely similar in vestiture to those of *Oclemena reticulata* (Ell.) Nesom, a species of the coastal

plain of Alabama, Florida, Georgia, and South Carolina, far-removed in geography and habitat from the other species of the genus. This cypselar vestiture is unlike that of *O.* ×*blakei* from elsewhere in its range or that of its parental species, which is glandular but usually otherwise glabrous; cypselae of *O. acuminata* rarely may be sparsely strigose (e.g., Pendleton Co., W. Va., *Musselman 3894*—NCU), and Semple et al. (1996) describe the cypselae of *O. nemoralis* as "sparsely strigose." The differences in non-glandular cypselar vestiture and the leaf margins are morphological differences separating *Gerdes 2210* from *O.* ×*blakei*, but the close correspondence in other morphological features suggests that an identification as *O.* ×*blakei* is a reasonable hypothesis for the Keweenaw Peninsula plants.

Identification as a separate species

In view of tentative evidence against a hypothesis of hybridity between *Oclemena nemoralis* and *O. acuminata* (considering the anomalous achene vestiture, unusual leaf morphology, and the unlikelihood of the establishment of *2210* through long-distance dispersal) for the origin of *2210*, a hypothesis that this population represents an independent evolutionary branch of *Oclemena* becomes plausible. If this were the true origin, recognition of *2210* at specific rank would be appropriate. Current evidence, however, does not convincingly support or eliminate either of the proposed hypotheses alternative to the originally proposed intergeneric hybridization. All three competing hypotheses will be further investigated after an upcoming field season, when it will be possible to make observations on pollen and fruit fertility and collect fresh material for molecular analysis.

ACKNOWLEDGMENTS

I am grateful to the staff of MICH for lending the collections from Houghton County, the staffs of GH and NCU for accommodation while working there, to Luc Brouillet for his comments on the plants involved and on an early version of the manuscript, and to an anonymous journal reviewer.

REFERENCES

Brouillet, L. and J.-P. Simon. 1981. An ecogeographical analysis of the distribution of *Aster acuminatus* Michx. and *A. nemoralis* Aiton (Asteraceae: Astereae). Rhodora 83:521–550.

Gerdes, L.B. 1998 [2000]. *Aster nemoralis* and the apparent hybrid *Aster nemoralis* ×*Aster umbellatus* in Houghton County, Michigan. Michigan Bot. 37:17–20.

Hill, L.M. 1976. Morphological and cytological evidence for introgression in *Aster acuminatus* Michx. in the Southern Appalachians. Castanea 41:148–155.

Hill, L.M. and O.M. Rogers. 1970. Chromosome numbers of *Aster blakei* and *A. nemoralis*. Rhodora 72:437–438.

Hill, L.M. and O.M. Rogers. 1973. Chemical, cytological and genetic evidence for the hybrid origin of *Aster blakei* (Porter) House. Rhodora 75:1–25.

Nesom, G.L. 1993. Taxonomy of *Doellingeria* (Asteraceae: Astereae). Phytologia 75:452–462.

Nesom, G.L. 1994a. Review of the taxonomy of *Aster* sensu lato (Asteraceae: Astereae), emphasizing the New World species. Phytologia 77:141–297.

Nesom, G.L. 1994b. Hybridization in the Astereae (Asteraceae). Phytologia 77:298–307.

Nesom, G.L. 2000. Generic conspectus of the tribe Astereae (Asteraceae) in North America, Central America, the Antilles, and Hawaii. Sida, Bot. Misc. 20:i-viii, 1–100.

Pike, R.B. 1970. Evidence for the hybrid status of *Aster Blakei* (Porter) House. Rhodora 72: 401–436.

Semple, J.C., J.G. Chmielewski, and C. Leeder. 1991. A multivariate morphometric study and revision of *Aster* subg. *Doellingeria* sect. *Triplopappus* (Compositae: Astereae): The *Aster umbellatus* complex. Canad. J. Bot. 69:256–276.

Semple, J.C., S.B. Heard, and C.S. Xiang. 1996. The Asters of Ontario (Compositae: Astereae): *Diplactis* Raf., *Oclemena* E.L. Greene, *Doellingeria* Nees and *Aster* L. (including *Canadanthus* Nesom, *Symphyotrichum* Nees, and *Virgulus* Raf.). Rev. ed. Univ. of Waterloo Biol. Ser. 38:i–viii, 1–94.

Voss, E.G. 1996. Michigan Flora. Part III, Dicots (Pyrolaceae–Compositae). Cranbrook Institute of Science Bull. 61 and Univ. of Michigan Herbarium, Ann Arbor.

Xiang, C. and J.C. Semple. 1996. Molecular systematic study of *Aster* s. lat. and related genera (Asteraceae: Astereae) based on chloroplast DNA restriction site analyses and mainly North American taxa. In: D.J.N. Hind and H.J. Beentje, eds. Compositae: Systematics. Proc. Interntl. Compositae Conf., Kew, 1994. Vol. 1, pp. 393–423.